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Notes on Appearance and Speculated Behavior of the O'ahu 'Ō'ō (Meliphagidae)[1]

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ABSTRACT: The O'ahu 'Ō'ō (*Moho apicalis*) was last collected in 1837, and is one of the rarest Hawaiian birds in museum collections. Despite the cultural importance of the 'Ō'ō as a source of yellow feathers for Hawaiian featherwork, next to nothing is known about this species. A pair of these extinct honeyeaters at the Museum für Naturkunde der Humboldt-Universität in Berlin have conspicuous yellow bare orbital rings, features not previously noted or illustrated. Individuals apparently varied in the expression of this character, because six other specimens did not have the yellow ring. Possible sources of variation include age, sex, agonistic state, and breeding condition. That this character varies with age is suggested by its presence in a reduced form in juveniles of other 'Ō'ō species. Increased sexual dimorphism of the modified tails relative to body size in this and other 'Ō'ō species indicates sexual selection on tails either from intrasexual aggression or intersexual mate choice. Patterns of contrasting yellow feather tufts differ between birds from different islands, but not between sexes, suggesting that males and females experienced similar evolutionary pressures for this feature. The 'Ō'ō's tail may have evolved under the influence of sexual selection on males, and the conspicuous yellow feather tufts by social selection experienced equally by both sexes.

THE O'AHU 'Ō'ō (*Moho apicalis*) is one of the rarest Hawaiian birds in museum collections. Thousands must have been captured for the yellow and black feathers used in Hawai'i's famous feather cloaks, leis, and images, but very few individuals were ever obtained for scientific studies. Only 10 specimens apparently remain of this distinctive honeyeater, last collected in 1837, and which already may have been extinct by the time it was described in 1860 (Gould 1860).

Because the specimens are now scattered among museums in North America and Europe, it has been difficult to determine exactly how many O'ahu 'Ō'ō specimens exist. Published accounts disagree on the number, reporting five to eight individuals. Wilson and Evans (1890–1899) recorded only five specimens, three in England and two in Vienna. Rothschild (1893–1900) noted six specimens, adding one in Berlin to the above list. Greenway (1967) cited at least eight examples in Berlin; Cambridge, Massachusetts; London (2); New York (2); Paris; and Vienna. Banko (1979, 1981) listed eight specimens in five cities: Cambridge, Massachusetts; London (2); New York (2); Paris; and Vienna (2). Based on specimens I examined and correspondence with museum curators, I have documented 10 specimens: a pair each in Berlin, London, and New York; and single birds in Cambridge, Massachusetts; Chicago; Paris; and Vienna. I examined two specimens of the O'ahu 'Ō'ō at the Museum für Naturkunde der Humboldt-Universitat in Berlin and compared them with specimens in New York, Cambridge, and London and with specimens of other 'Ō'ō species in these and other cities. Here I document previously overlooked aspects of the O'ahu 'Ō'ō's appearance and speculate on their possible function.

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MATERIALS AND METHODS

Specimens of O'ahu 'Ō'ō were examined in Berlin in April and October 1996, in New York and Cambridge in July 1997, and in London in December 1997. 'Ō'ō specimens from Hawai'i (*Moho nobilis*), Kaua'i (*M. braccatus*), and Moloka'i (*M. bishopi*) were also examined in those cities, and in Cambridge, Dresden, Frankfurt, Los Angeles, Philadelphia, and Washington, D.C., between April 1996 and August 1997. See acknowledgments for museums visited and their standard abbreviations used hereafter.

The following morphological measurements were recorded: unflattened wing chord, tail length, tarsus length, length of exposed culmen, and length of bill from gape to tip. Wing and tail were measured with a ruler to the nearest 0.5 mm; the tarsus was determined with dividers and measured to the nearest 0.5 mm on the ruler; and bill measurements were taken with dial calipers to the nearest 0.001 inch and then converted to the nearest 0.1 mm.

Capitalized, numbered colors were matched to Smithe (1975) as a color standard.

RESULTS

The two O'ahu 'Ō'ō in Berlin are in excellent condition and have been given glass eyes, rendering them eerily lifelike. They have red ZMB type labels, but the designations as type specimens have been crossed out. A label on one specimen indicates that it was collected by Deppe, but there is no further information for either bird. Both specimens may have been collected by Ferdinand Deppe in 1837, as were many other old O'ahu specimens in the Berlin Museum. Deppe resided in Nu'uanu Valley while collecting with the American naturalist John K. Townsend (Townsend 1839), so the specimens may have come from there.

Sex and Size

Neither specimen has the sex determined, but one is roughly 20% larger than the other (Figure 1, Table 1). Because the O'ahu 'Ō'ō, like other 'Ō'ō species and other honeyeaters (Wilson and Evans 1890–1899), exhibited sexual size dimorphism, with males roughly one-fourth larger than the females (Gould 1860), these birds are probably a male and female. The larger specimen (ZMB 7851) is here referred to as male and the smaller (ZMB 7852) as female.

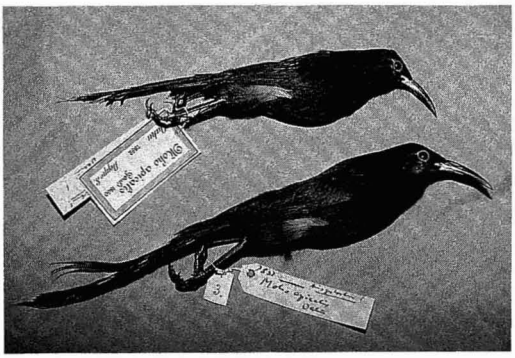

FIGURE 1. O'ahu 'Ō'ō pair in Berlin: ZMB 7852 (*above*) and ZMB 7851.

TABLE 1

MEASUREMENTS OF O'AHU 'Ō'ō SPECIMENS IN BERLIN

MEASUREMENTS (in mm)	SPECIMEN 7851	SPECIMEN 7852	SIZE RATIO (7851/7852)
Right wing	120.0	98.5	1.21
Tail from tip to insertion of quill	151.0	113.0	1.33
Right tarsus to last undivided scute	35.5	30.5	1.16
Exposed culmen	33.5	27.4	1.22

NOTE: Wing and tail measured with ruler to nearest 0.5 mm. Tarsus determined with dividers and measured to nearest 0.5 mm on ruler. Bill measurements taken with calipers to nearest 0.001 inch and converted to nearest 0.1 mm.

Color and Appearance

Both specimens are sooty brownish black. None of Smithe's (1975) colors matched exactly: the body is intermediate between Blackish Neutral Gray (82), Sepia (119), and Fuscous (21); the throat is closest to Jet Black (89); the crown is glossy black in con-

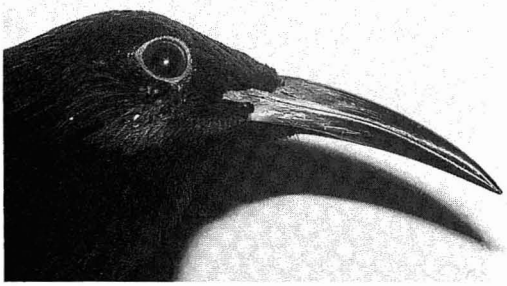

FIGURE 2. Close-up of face of male (ZMB 7851), showing pale bare orbital ring and pale base of bill.

trast to the duller colors of the body; and the bright yellow feathers of the flanks and undertail coverts are closest to Spectrum Yellow (55).

Both specimens have an obvious yellow ring of bare skin, close to but paler than Sulfur Yellow (157) surrounding the eyes (Figure 2), a prominent feature that seems not to have been noted previously. The orbital skin showed no trace of feathers when examined with a dissecting microscope at 12.6 and 20 power. The skin appeared dried and flaky, and yellow skin was clearly visible beneath and between feathers scattered behind the orbital ring. Perhaps most important, the orbital rings of the two specimens differ slightly in color: the male's are slightly yellower than the female's.

A Hawai'i 'Ō'ō (*Moho nobilis*) specimen (ZMB 15406) of comparable age with glass eyes had a much smaller orbital ring that was clearly black, in contrast to those of the O'ahu birds. Other specimens of Hawai'i 'Ō'ō, Kaua'i 'Ō'ō or 'Ō'ō 'ā'ā (*M. braccatus*), and Moloka'i 'Ō'ō (*M. bishopi*) also had dark orbital skin. Examination of two specimens of O'ahu 'Ō'ō at the American Museum of Natural History (AMNH 306357, AMNH 459000) in New York, one at the Museum of Comparative Zoology (MCZ 17598) in Cambridge, Massachusetts, and two at the British Museum of Natural History in Tring (BMNH 1860.11.26.51, BMNH 19a [Vellum Cat.]) showed only a black or dark brown orbital ring. A mounted female at the Museum National d'Histoire Naturelle in Paris (E. Pasquet, pers. comm.) and a specimen at the Field Museum of Natural History in Chicago (D. Willard, pers. comm.) also lack yellow rings.

Unfortunately, there seem to be no written descriptions of the O'ahu 'Ō'ō in life, and the specimens I examined do not have any attached data to indicate colors of the soft parts. Based on the five individuals I examined and information received from other museums, it appears that the yellow orbital ring is found only in the Berlin specimens.

Although the orbital rings were dark in the three American specimens I examined, dull yellowish skin was visible under the feathers below the eye and around the gape in each. Also, the area behind the eye was covered by short, velvety feathers in the Moloka'i and Hawai'i 'Ō'ō, as well as those O'ahu 'Ō'ō that lacked bare yellow skin. In addition, yellow skin was prominent where feathers had fallen out along the shoulder in a specimen (MCZ 10993) of the Hawai'i 'Ō'ō and was also visible under the feathers below the eye and around the gape in several other specimens.

The 'Ō'ō bills in Berlin were yellowish basally, a possible indication of immaturity, because the adults of other 'Ō'ō species had all-black bills. Three juvenile specimens (AMNH 693927, 693928, 693955) of the Kaua'i 'Ō'ō had distinctly yellowish or yellow brown lower bills and legs, which contrasted with the black bills and legs of adult specimens. These juveniles also had some bare yellow skin showing on the face near the gape and behind the eye, but this patch was not as distinct or conspicuous as in the O'ahu 'Ō'ō in Berlin.

There was no evidence of a predefinitive (subadult) plumage in specimens of any of the 'Ō'ō species I examined: individuals were in juvenile or adult plumage, with no obvious intermediate plumages.

Auricular Tufts

The Berlin specimens have elongated auricular tufts (Figure 2), which were slightly

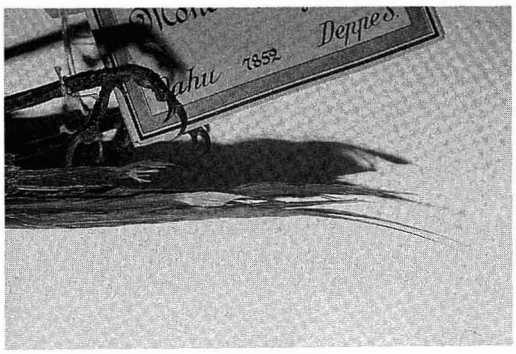

FIGURE 3. Close-up of tail of female (ZMB 7852).

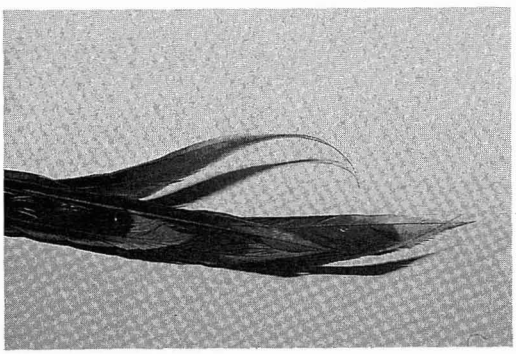

FIGURE 4. Close-up of tail of male (ZMB 7851).

paler and more dusky than the rest of the face. The striking Moloka'i 'Ō'ō (illustrated in sources cited above for O'ahu 'Ō'ō) was most notable for the prominent yellow auricular tufts, not found in other species. The Berlin specimens show that such tufts existed in a much smaller form on the O'ahu birds. Specimens of Kaua'i 'Ō'ō in Berlin also have inconspicuous auricular tufts, even smaller than those of the O'ahu birds. No auricular tufts were visible on the Hawai'i 'Ō'ō specimens.

Tail Shape

All O'ahu specimens have a long, graduated tail. Except for the central pair, each feather is tipped below with white (see illustration in Rothschild [1893–1900], Shallenberger [1978]). The central pair is highly attenuated, becoming wirelike near the tips. Although in some birds such ornamentation involves modified upper tail covert feathers (e.g., the long "tail" of the Resplendent Quetzal, *Pharomachrus mocinno,* illustrated in Howell and Webb [1995]), examination under the dissecting microscope revealed that the attenuated feathers of the O'ahu 'Ō'ō are the central retrices. Tail shape differed between the Berlin male and female: in the female the tips curve up, as illustrated in most sources; they were ca. 15 mm longer than the rest of the tail (Figure 3). In the male, however, the tips curve up and then curl down in a distinctive manner not seen in any published illustrations; they were ca. 15 mm shorter than the rest of the tail (Figure 4). The New York and London males and females had the wirelike central retrices curved up as in the Berlin female; these were slightly longer in the female and slightly shorter in the male than the rest of the tail. The tail was damaged in the Cambridge specimen, but the central retrices appeared to resemble the tails of the New York specimens.

The Moloka'i and Hawai'i 'Ō'ō also have long tails with modified central retrices, but these are twisted laterally and neither attenuated nor wirelike as in the O'ahu 'Ō'ō. In contrast, the Kaua'i 'Ō'ō has a shorter, less modified tail that resembles that of a woodpecker, apparently functioning as a brace in climbing tree trunks (Perkins 1903).

DISCUSSION

All illustrations of O'ahu 'Ō'ō available to me show an entirely black face with no traces of yellow (Wilson and Evans 1890–1899 [reprinted in Wilson and Buff 1989], Rothschild 1893–1900 [reprinted in Shallenberger 1978], Pratt et al. 1987 [which was based on earlier illustrations]). Because of the striking nature of this eye patch, it seems odd that it has not been illustrated or described previously. Possible sources of variation and function of this feature are therefore of interest, particularly with regard to signaling. Potential sources of variation in skin color include age, breeding

condition, aggressive state, and museum preparation.

It is possible that the yellow skin is apparent in the Berlin specimens because of their good condition and glass eyes. Specimens with cotton protruding from the eyes, the most common preparation practice, may have the eye patch obscured, but it seems unlikely that differences in preparation would hide all traces of the orbital skin. The New York specimens also have glass eyes, but lack the yellow orbital skin. It is unlikely that the yellow orbital ring is caused by fading of dark skin over time. And because bare parts often darken over time in museum specimens (e.g., Engilis et al. 1996, Lepson 1997), the bare skin was probably brighter and more prominent in life. Moreover, bare skin is still yellowish or orangish in old specimens of other honeyeaters, such as the Wattled Honeyeater (*Foulehao procerior,* MCZ 81984 from 1899), Yellow-throated Miner (*Manorina flavigula,* AMNH 694462 from 1903, AMNH 694455 from 1907), and Tawny-breasted Honeyeater (*Xanthotis flaviventer,* MCZ 81728 from 1910).

Orbital Rings: Fact or Artifact?

It has been suggested that the yellow orbital rings on the Berlin specimens might not be real features, but painted artifacts (S. L. Olson, in litt.), as was common in the past, particularly with specimens mounted for display, as was apparently the case for this pair. The orbital rings could have been painted yellow by a preparator who thought they would harmonize with the yellow feathers of the flanks.

Painted skin should be obvious with appropriate examination (S. L. Olson, pers. comm.; M. LeCroy, pers. comm.), but study of the orbital rings with a dissecting microscope showed no signs of paint, lacking the differences in color one would expect if paint had worn off or cracked over time. Even the most careful preparator would be likely to accidentally touch some of the surrounding feathers with paint, but no trace of paint is visible on any of the feathers. Perhaps most important is the difference in color between the orbital rings of the two specimens: that the individuals naturally differed in color is a more credible observation than a paint job.

The bare yellowish skin seen under the feathers near the eyes of the American O'ahu 'Ō'ō specimens and on some individuals of other species may indicate that yellowish skin is the underlying condition in 'Ō'ō, with exposed skin being black on some O'ahu birds and on the other species. The short, velvetlike feathers around and behind the eye in specimens lacking the bare orbital ring might easily molt out, suggesting a mechanism for individual differences in the expression of this character.

Possible Function of Bare Skin in Life History

What was the role of bare orbital skin in the life history of the O'ahu 'Ō'ō, especially because there is evidence of individual differences in orbital ring color? One possibility is that color of the orbital skin was age-related. In other honeyeaters, age-related differences in facial skin color are known in several genera, among these *Entomyzon* and *Melithreptus* (illustrated in Beehler et al. [1986] and Slater et al. [1986]). In the O'ahu 'Ō'ō, the eye patch may have become yellow only in adults and functioned in sexual or social signaling. Alternatively, it may have been yellow in young birds, indicating age and behavioral subordinance, and either disappearing (by becoming feathered) or turning black in adults. In Black-billed Magpies (*Pica pica*), juveniles possess a patch of bare yellow skin behind the eye that disappears as they mature (Lawton and Lawton 1986), and several species of neotropical jays (*Cyanocorax*) have yellow bills and orbital rings that turn black with age (Hardy 1973, illustrated in Howell and Webb [1995]). Similarly, the juvenile Long-billed Honeyeater (*Melilestes megarhynchus*) of New Guinea has a yellow eye ring that disappears when adult, but this is feathered rather than bare (Beehler et al. 1986).

Early sources (Wilson and Evans 1890–1899, Rothschild 1893–1900) reported that immatures of other 'Ō'ō species lacked

the yellow plumes so famous in Hawaiian featherwork. Because the Berlin specimens do possess the yellow feathers, they are not likely to be juveniles. But the plumage may have matured before the facial skin, and the Berlin pair may have been second-year or third-year individuals. Because there does not appear to be a predefinitive (subadult) plumage in other 'Ō'ō species, the birds may have acquired their adult plumage in the first molt after fledging. Plumage might only distinguish juveniles, with younger adult birds retaining the yellow skin as a signal of possible subordinate status relative to older birds. This occurs in the Yucatan Jay of Mexico (*Cyanocorax yucatanicus*), which has a highly distinctive, but briefly held, juvenile plumage. After molting into adult plumage, however, young birds retain the yellow bill and orbital ring for up to two more years before they turn black as in older adults (Howell and Webb 1995).

Several features support this possibility in the O'ahu 'Ō'ō. The yellowish bases of the bills may be a sign of immaturity because juvenile specimens of Kaua'i 'Ō'ō have yellowish bills and legs. And the juvenile specimens have some bare yellowish skin visible near the eye, not evident in adult specimens. Although these are not discrete rings as in the O'ahu birds, they suggest a mechanism for age-variable expression of this character, wherein the feathers might grow after the first years of life, with the yellow skin signaling a younger age.

Bare facial skin may also function to signal breeding condition or aggressive state. In the Brown Honeyeater (*Lichmera indistincta*), males have a yellow gape that turns black in the breeding season (Slater et al. 1986). More unusual is the Common Smoky Honeyeater (*Melipotes fumigatus*), which possesses a large bare circumorbital patch that is usually yellow, but can turn orange or red when flushed with blood (Beehler et al. 1986) and which likely functions in aggressive or sexual interactions. Orbital ring color might thus have changed color to signal breeding state in the O'ahu 'Ō'ō. Alternatively, adults might have molted out the short, velvety feathers around the eye when coming into breeding condition, thus exposing the underlying yellow skin. Nesting has only been observed for the Kaua'i 'Ō'ō, and there is no mention of color changes (Berger 1981), nor have seasonal changes been noted in other 'Ō'ō species (Perkins 1903, Munro 1944).

Honeyeaters frequently have bare skin near the eyes or elsewhere on the face (see illustrations in Beehler et al. [1986], Slater et al. [1986]). These contrasting patches probably act as important signaling devices in this aggressive, primarily nectarivorous family. Similarly, contrasting facial skin in the O'ahu 'Ō'ō may also have performed signaling functions, as may be the case for the conspicuous yellow feather tufts in this and other 'Ō'ō species. Although no other 'Ō'ō species had contrasting facial skin, the Kaua'i 'Ō'ō had conspicuous whitish irises, and the Moloka'i 'Ō'ō had long yellow auricular tufts, which may also have functioned as signals in these species.

Possible Behavioral Functions of Tail Shape and Plumage Pattern

Almost nothing is known of O'ahu 'Ō'ō behavior. The only information comes from Andrew Bloxam, who collected on O'ahu in 1825. Even this is of captive birds, because he never saw the species in the wild (quoted in Olson [1996:14]): "There are two or three varieties of this bird or probably the difference of age may cause a difference of appearance among them. This however is very slight. Their note is a harsh chirp of two or three different tones. They feed principally on the flowers of the *Eugenia Malaccensis.* I kept some alive which the natives brought me, tho' almost entirely destitute of feathers, for three or four weeks, feeding them principally upon sugar & water. They took flies, however, which came into their cage, with great quickness & adroitness." Because it was not known at the time that there was more than one species of 'Ō'ō, it is unclear whether Bloxam's remarks on appearance referred to variation within the O'ahu 'Ō'ō or to differences between it and the Hawai'i 'Ō'ō (the Kaua'i and Moloka'i species were not yet known).

Long graduated tails are aerodynamically costly (Balmford et al. 1993) and probably evolved with a signaling function, the benefits of which logically must outweigh the energetic costs of such a tail. The O'ahu 'Ō'ō tail feathers are somewhat reminiscent of those of lyrebirds (Menuridae), particularly females (see Slater et al. 1986), so perhaps the 'Ō'ō's modified tail served in courtship displays, as they do for the lyrebirds (Pizzey 1980). The only information on courtship of any 'Ō'ō species comes from Perkins (1903: 441–442), who stated that "when in the company of its mate" (no sex was indicated) the Hawai'i 'Ō'ō frequently raised its long tail and wings, showing the yellow axillary tufts, and that it had "various other postures and antics," and Henshaw (1902:71), who wrote that the male would "jet its long tail ... to reveal its bright yellow under tail-coverts to its no doubt admiring mate."

Alternatively, or additionally, the tails may have served in agonistic interactions. Perkins (1903: 441) eloquently described the aggressive behavior of the Hawai'i 'Ō'ō: "In attacking the other nectar-eating birds it makes a savage rush on the one that excites its animosity, and as in making this attack it frequently raises its tail with the long twisted feathers, and also raises its wings, so that the yellow axillary feathers and under-tail coverts of the same colour can be distinctly seen, it presents a very fine appearance." The O'ahu 'Ō'ō likely used its modified tail in a similar manner while defending feeding or nesting territories.

Separate functions for the long tail and the yellow feathers may also be possible. In the Scarlet-tufted Malachite Sunbird (*Nectarinia johnstoni*) of East Africa, the male pectoral tufts function in territorial defense of flowering lobelias, and the elongated tail in mate choice (Evans and Hatchwell 1992*a,b*). The observations by Perkins (1903) apparently indicate that both signals were used simultaneously in the 'Ō'ō. However, because both sexes have the yellow tufts, these tufts are more likely to serve a social function that is common to both sexes, such as defense of food resources, and probably evolved via social selection. The larger tail of the male, disproportionate to its larger body size (Tables 1, 2), indicates a difference in selective pressures on the sexes, probably due to sexual selection on the male, either to attract females or in aggressive interactions with other males.

The evolution of conspicuous signals may be advantageous to species that defend temporally variable resources, such as nectar. In the Hawaiian honeycreepers (Drepanidinae), the primarily nectarivorous species, such as the Mamo (*Drepanis pacifica*) and 'I'iwi (*Vestiaria coccinea*), also show aggressive behavior and typically conspicuous, highly contrasting, sexually monomorphic plumage. Nectar-feeding specialists must often contend with resource patches, such as stands of 'ōhi'a lehua (*Metrosideros polymorpha*) or seasonally flowering lobelioids (Campanulaceae), the profitability of which varies throughout the year. Indeed, the 'Ō'ō's extreme foraging specialization and large size might have constrained it to forage on only the richest resource patches, as has been proposed for the 'I'iwi (Pimm and Pimm 1982). Also, the two largest species coexisted with the Mamo (*Drepanis pacifica* on Hawai'i and *D. funerea* on Moloka'i), which were the largest nectarivorous Hawaiian honeycreepers. Conspicuous visual and vocal signaling may alert subordinate birds to the presence of dominants and thus reduce energetically costly aggressive interactions. The other 'Ō'ō species were described as aggressive and territorial, driving out all other competitors from favored feeding trees (Perkins 1903, Conant et al. in press). Perkins (1903:441) reported of the Hawai'i 'Ō'ō, "It is very intolerant of the scarlet Iiwi (*Vestiaria*), and will at intervals suspend its feeding to chase away any of these that have ventured into its own tree, or it will even leave this, however profuse be the blossoms, to drive from some distant tree one that it has chanced to spy there. This aggressiveness appears so wanton and unnecessary, and so frequently interrupts its own feeding, that one suspects it must be an ancient habit, which has survived from a time when either nectar-producing flowers were scarcer, or the birds which fed upon them much more numerous."

TABLE 2

SEXUAL DIMORPHISM OF 'Ō'ō SPECIES

MEASUREMENTS (in mm)	SIZE RATIO[a]			
	Kaua'i	O'ahu	Moloka'i	Hawai'i
Wing	1.08 (14 M, 19 F)	1.15 (4 M, 3 F)	1.13 (17 M, 4 F)	1.18 (35 M, 29 F)
Tail	1.10 (12 M, 18 F)	1.17 (4 M, 3 F)	1.23 (13 M, 3 F)	1.47 (32 M, 27 F)
Tarsus	1.06 (15 M, 19 F)	1.12 (4 M, 3 F)	1.13 (17 M, 4 F)	1.14 (32 M, 26 F)
Culmen	1.08 (12 M, 19 F)	1.16 (4 M, 3 F)	1.16 (15 M, 4 F)	1.18 (33 M, 28 F)
Gape-tip	1.06 (7 M, 15 F)	1.14 (4 M, 3 F)	1.14 (15 M, 4 F)	1.16 (28 M, 24 F)

NOTE: Methods as in Table 1 from specimens at AMNH (3 F, Kaua'i; 1 M, 1 F, O'ahu; 9 M, 2 F, Moloka'i), ANSP (8 M, 6 F, Hawai'i), BMNH (6 M, 11 F, Kaua'i; 1 M, 1 F, O'ahu; 4 M, 1 F, Moloka'i; 5 M, 6 F, Hawai'i), CMZ (2 M, 2 F, Kaua'i; 3 M, Moloka'i; 4 M, 4 F, Hawai'i), MCZ (1 M, 2 F, Kaua'i; 1 M, O'ahu; 2 M, Moloka'i; 8 M, 3 F, Hawai'i), NMNH (2 M, 2 F, Kaua'i; 8 M, 4 F, Hawai'i), SMF (1 M, Kaua'i), SMFT (1 M, Kaua'i; 2 M, Hawai'i), and ZMB (3 M, 1 F, Kaua'i; 1 M, 1 F, O'ahu; 7 M, 3 F, Hawai'i).

[a] Male [M]/female [F]; sample sizes in parentheses.

Color patterns differ arbitrarily between the 'Ō'ō species. The Kaua'i 'Ō'ō was small, with whitish eyes, a conspicuous white bend of the wing, and yellow plumage confined to the thighs; the O'ahu 'Ō'ō had yellow orbital rings, yellow flanks, and a white-tipped tail; the Moloka'i 'Ō'ō had yellow auricular and small axillary plumes; and the Hawai'i 'Ō'ō had yellow axillary plumes and under-tail coverts. Such arbitrary differences in color pattern between closely related species are often considered as having arisen through sexual or social selection and then exaggerated for species recognition (West-Eberhard 1983, Andersson 1994). This would be consistent with the modified tails and yellow feathers serving in courtship and/or territorial aggression. It also would account for the arbitrary differences between the 'Ō'ō species in those characters: because social selection is predicted to be nondirectional, it simply favors distinctive signals (West-Eberhard 1983).

CONCLUSIONS

The yellow orbital rings are perhaps the most striking feature of the Berlin specimens of O'ahu 'Ō'ō but are apparently absent in other specimens. Because of the lack of noticeable paint, the yellow skin visible beneath the feathers near the eye, and color differences between the specimens, I conclude that the yellow orbital rings were actual features of these specimens of the O'ahu 'Ō'ō. Because bare yellowish skin is most evident on juveniles of other 'Ō'ō species, these orbital rings may only exist in younger adults, functioning to signal age and lower status relative to older birds with black orbital rings. That the yellow orbital rings were a signal of youth is also suggested by the pale bases of the bills because juvenile 'Ō'ō specimens had yellowish bare parts.

It is tempting to ascribe the marked difference in tail shape between the Berlin specimens to sexual dimorphism, but the pair in New York resembled each other. Thus, the difference I observed in Berlin appears to be due to individual variation, possibly as a result of differing degree of feather wear. Sexual size dimorphism is greatest in the tails, indicating that selection for longer tails was strongest in males, suggesting sexual selection either by aggression between males or mate choice by females.

The inconspicuous auricular tufts on the O'ahu 'Ō'ō and Kaua'i 'Ō'ō apparently illustrate a trend for the elongation of this character, which is fully expressed in the striking Moloka'i 'Ō'ō. The differing patterns of contrasting yellow feathers between 'Ō'ō species is consistent with social selection acting on both sexes to exaggerate arbitrary signals for social competition in the different species.

Unfortunately, the speculations presented here on the life history of the O'ahu 'Ō'ō will always remain just that. The extinction of the entire genus means that there will never be an opportunity to test any of the proposed signaling functions of 'Ō'ō skin color and dimorphism. Studies of these conspicuous and aggressive birds might have made important contributions to further understanding mechanisms of mate choice, status signaling, and social competition. The loss of the fabled 'Ō'ō species is not merely a historical footnote or curiosity, but is also a cultural and scientific tragedy.

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